

## Historical Biogeography of Tamarins, Genus *Saguinus*: The Molecular Phylogenetic Evidence

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**ABSTRACT** Hypotheses of the historical biogeography of tamarins (genus *Saguinus*) based on variation in coat colors and body size are tested using phylogenetic relationships inferred from mitochondrial DNA (mtDNA) sequence data. Samples from all 12 species of *Saguinus* and several subspecies are included in the analysis. Approximately 1,200 bases of mtDNA sequence from the cytochrome *b* and D-loop regions are reported for the tamarins and several outgroup taxa. Parsimony analysis of the mtDNA sequence data reveals *Saguinus* to be a monophyletic taxon composed of two major clades: one, the Small-bodied clade, contains *S. nigricollis*, *S. tripartitus*, and *S. fuscicollis*, and the other, the Large-bodied clade, contains the other nine species. The phylogenetic relationships among tamarins inferred from the mtDNA sequence data reject previous hypotheses for the historical biogeography of tamarins and suggest different dispersal routes for this group of New World monkeys. The molecular data suggest that tamarins dispersed across South America in two major waves from an origin somewhere south of the Amazon. One wave moved in a westerly direction, whereas the other moved in a northeastern direction toward the Amazon delta and then west along the northern portion of the continent into northern Colombia and Panama. *Am J Phys Anthropol* 108:65–89, 1999. © 1999 Wiley-Liss, Inc.

Of the South American primate genera, *Saguinus* is one of the largest in numbers of species and geographical distribution (Hershkovitz, 1977). Tamarins are thought to be most closely related to the marmosets (*Callithrix* and *Cebuella*), the lion tamarins (*Leontopithecus*), and Goeldi's monkey (*Callimico*) (Hershkovitz, 1977; Mittermeier and Coimbra-Filho, 1981; Rylands et al., 1993; Jacobs et al., 1995). The phylogenetic relationships among the five aforementioned genera are not well resolved, and much debate exists concerning their proper taxonomic affiliations. Hershkovitz (1977) and others (Mittermeier and Coimbra-Filho, 1981; Ford, 1986; Rylands et al., 1993) place *Saguinus*, *Callithrix*, *Cebuella*, and *Leontopithecus* in the family Callitrichidae

and *Callimico* in the Family Callimiconidae. Some (Rosenberger, 1981a; Schneider et al., 1993; Harada et al., 1995), however, would place all five genera in the subfamily Callitrichinae of the family Cebidae. Regardless of the higher-level taxonomy, most would agree that tamarins, marmosets, and *Callimico* form a monophyletic group.

There are twelve recognized species of tamarins, ranging from the Amazon basin northward into Panama (Hershkovitz, 1977; Mittermeier and Coimbra-Filho, 1981; Thorington, 1988; Moore and Cheverud, 1992;

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Rylands, 1993). Tamarins are typically found in edge and secondary forest habitats. Most of the species are allopatric, with the most notable exception being *S. fuscicollis*, which is sympatric with other tamarin species throughout much of its range (Fig. 1). The most common boundaries between taxa are rivers (Peres et al., 1996), and Ayres and Clutton-Brock (1992) report that rivers wider than about 0.3 km are sufficient barriers to tamarin dispersal.

In his classic volume on New World monkeys, Hershkovitz (1977) proposed the dispersal routes for *Saguinus* shown in Figure 2A. The ancestral tamarin was postulated to have arisen in the central Amazon basin in the general vicinity of the current distribution of *S. fuscicollis* and subsequently to have spread northeast across the Amazon to give rise to *S. midas* and *S. bicolor*. Another wave of dispersal north along the Andes was proposed to have resulted in the extant species in northern Colombia and Panama. This hypothesis is based largely on the principle of metachromism and the current distribution of *Saguinus*. Metachromism is a theory of mammalian coat color evolution that Hershkovitz developed, in part, from his studies on geographic variation in pelage among tamarins (Hershkovitz, 1968, 1977). According to the theory, the primitive state for mammalian coat color is agouti and can evolve in an orthogenetic fashion through either of two color pathways, both leading finally and irreversibly to white. The phenomenon is proposed to be geographic and phylogenetic (Hershkovitz, 1968, 1977). However, because of extensive parallelisms among species, coat color is thought not to be a reliable phylogenetic character for distinguishing evolutionary relationships among species (Shedd and Macedonia, 1991; Jacobs et al., 1995). A hypothetical phylogeny constructed from Hershkovitz's (1977) description of species relationships based on the theory of metachromism and biogeography is shown in Figure 3A. He applied the theory of metachromism to subspecies relationships as well. The largest of the subspecies groups is *S. fuscicollis*; phylogenetic relationships predicted by Hershkovitz's (1977)

analyses of these subspecies are shown in Figure 3B.

An alternative to Hershkovitz's theory of dispersal has been proposed by Ferrari (1993a), based primarily on the hypothesis that callitrichids are phyletic dwarfs. Traditionally, callitrichids had been considered primitive due to their small size (and associated ecological characteristics) compared to other New World monkey families (Hershkovitz, 1977). However, according to the phyletic dwarfism hypothesis, the precursor to the callitrichid lineage was larger in body size than any of the extant species, which display a secondary reduction in body size (Ford, 1980; Leutenegger, 1980). Considering body-size differences and related ecological variables to be the most important factors in the evolutionary history of callitrichids (Ferrari, 1993b), Ferrari (1993a) formulated a theory of the phylogenetic relationships and dispersal of tamarins based on these factors.

Ferrari's (1993a) proposed dispersal of tamarins across the Amazon basin is depicted in Figure 2B. The ancestral tamarin, or prototype, is hypothesized to have been *midas*-like in size (average male size = 533 g [Fleagle and Mittermeier, 1980]) and is thought to have arisen in the general vicinity of the present *S. midas* distribution. From the lower Amazon, tamarins dispersed southwest, giving rise to the moustached tamarin group (*S. mystax*, *S. labiatus*, *S. imperator*). The final radiation of *Saguinus* would have given rise to the saddleback tamarins (*S. fuscicollis*). The origin of the species in northern Colombia and Panama (*S. oedipus*, *S. leucopus*, and *S. geoffroyi*) is not discussed. A hypothetical phylogeny based on Ferrari's (1993a) discussion of species relationships is shown in Figure 4A.

Although both of these dispersal theories are based, in part, on some hypothesis of the phylogenetic relationships among tamarins, neither of these studies utilized a phylogenetic data analysis. The purpose of this study is to test each of the above dispersal hypotheses for tamarins using phylogenetic evidence generated from mitochondrial DNA sequence data. The molecular phylogenetic

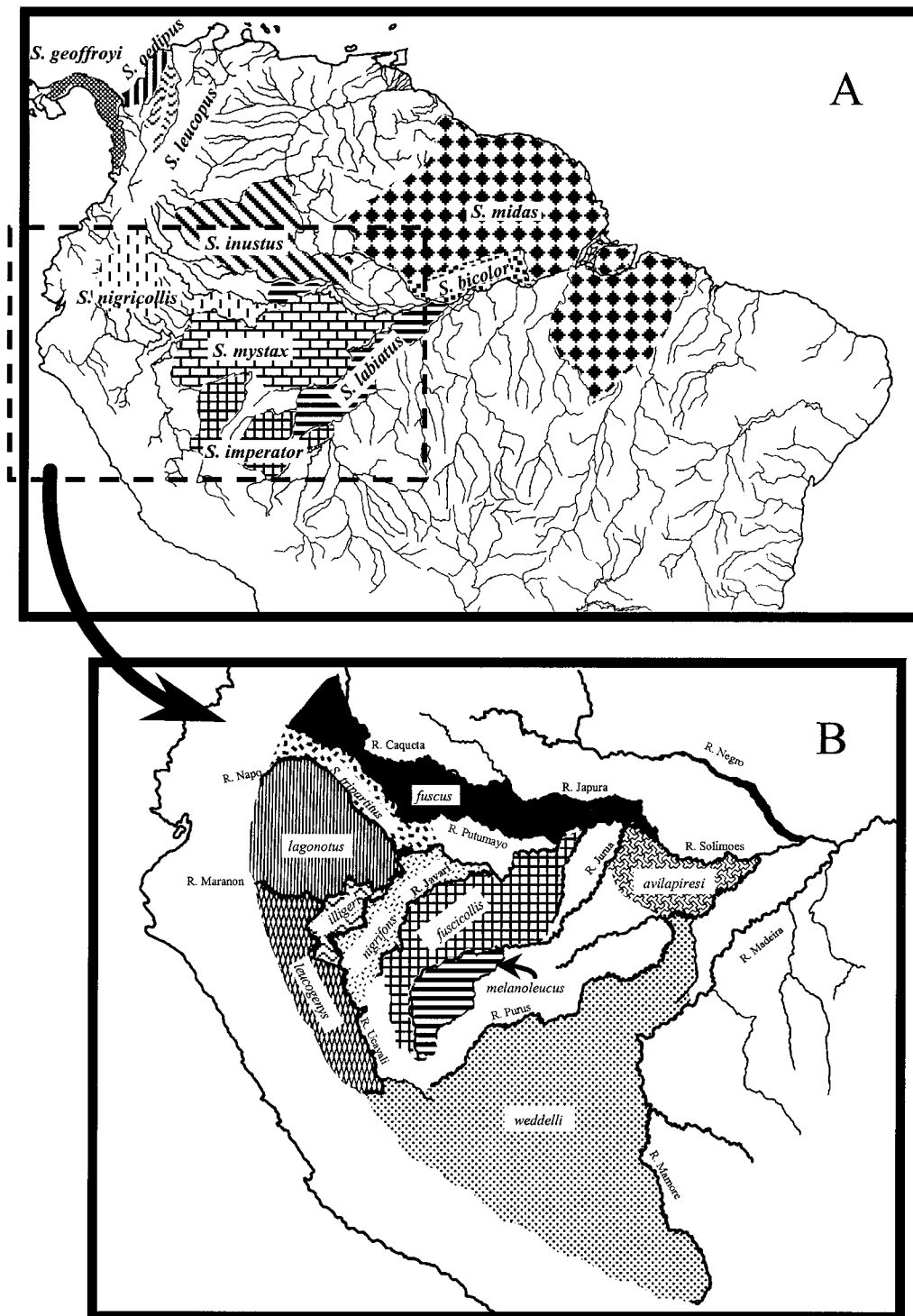


Fig. 1. Geographic distribution of *Saguinus* (with the exception of *S. fuscicollis* and *S. tripartitus*) **A**: and geographic distribution of *S. fuscicollis* subspecies and *S. tripartitus* **B**: based on Hershkovitz (1977) and others (for a review see Rylands et al., 1993).

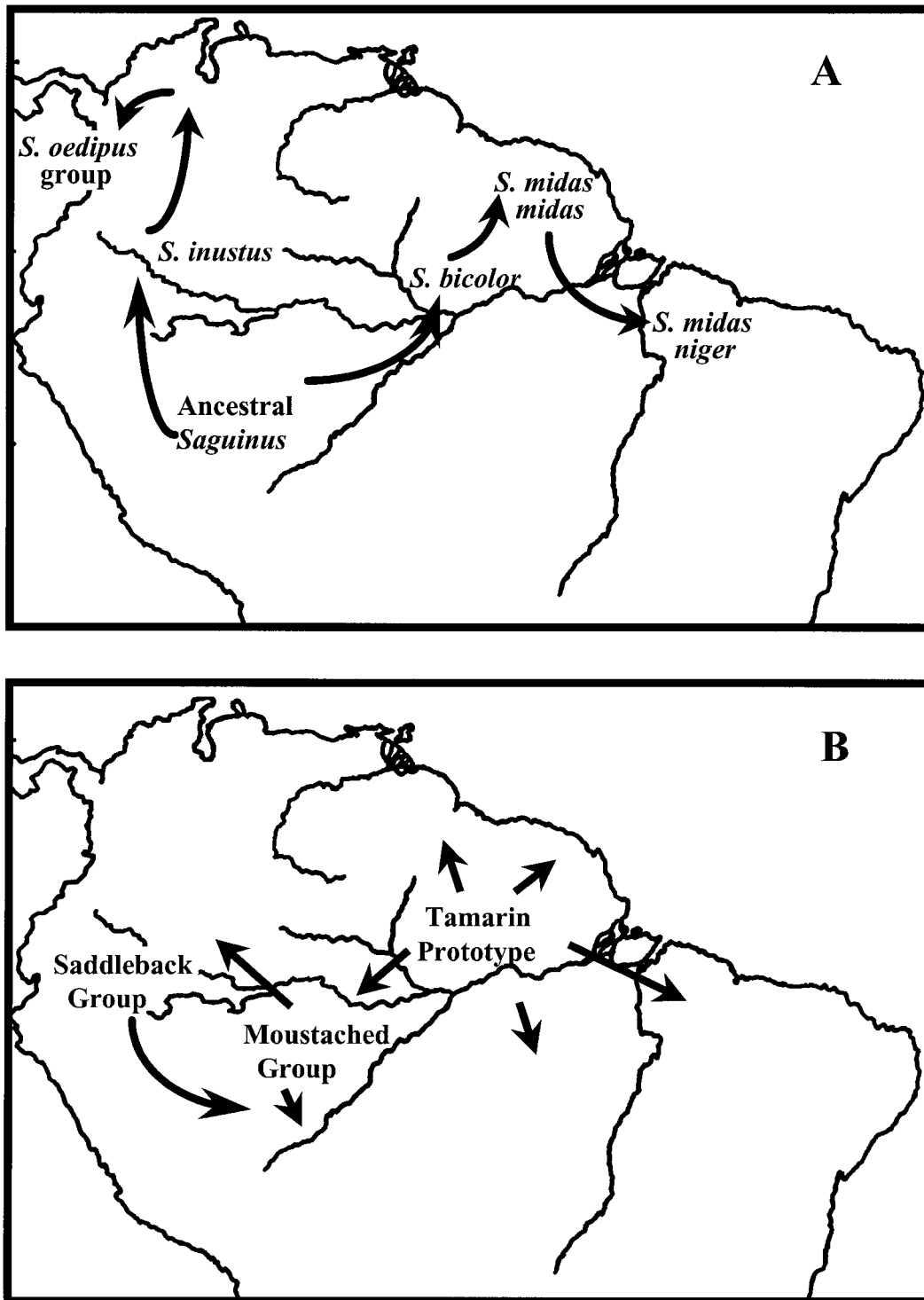


Fig. 2. Hypothesized historical dispersal routes for *Saguinus* based on Herskovitz (1977) **A**: and Ferrari (1993a) **B**.

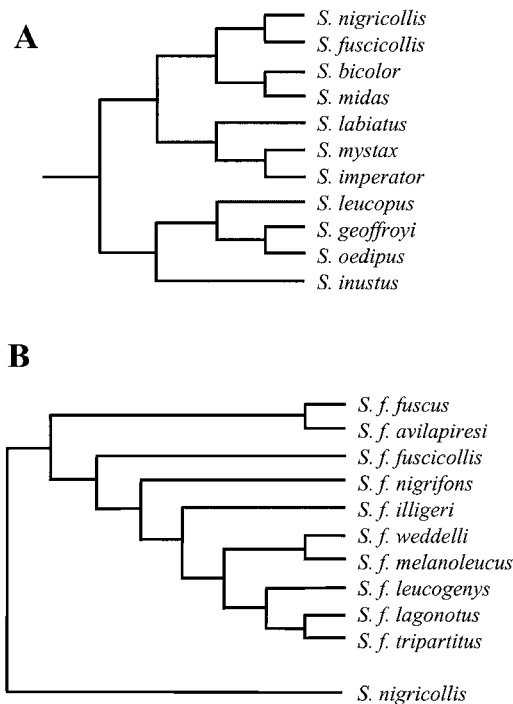


Fig. 3. **A:** Hypothetical phylogeny for *Saguinus* based on species relationships described by HersHKovitz (1977) (redrawn from Jacobs et al., 1995). **B:** Hypothetical relationships among the *S. fuscicollis* subspecies based on HersHKovitz (1977) (redrawn from Cheverud and Moore, 1990).

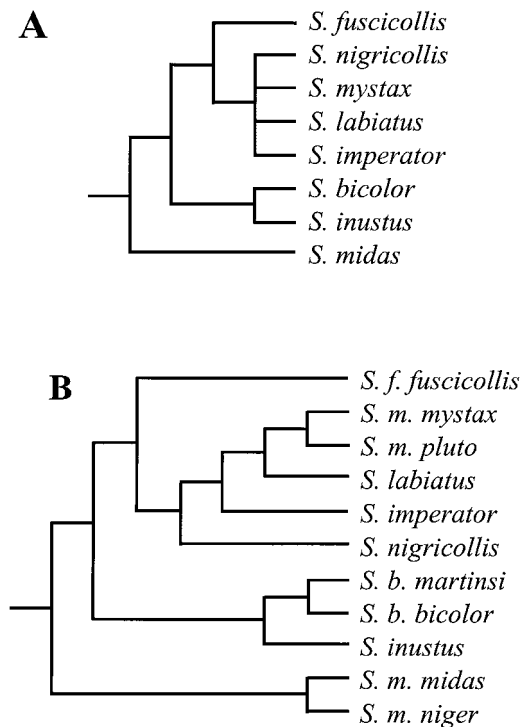


Fig. 4. **A:** The hypothetical phylogenetic relationships among *Saguinus* based on Ferrari's (1993) description of species relationships. **B:** The most parsimonious bifurcating tree (see Results) consistent with the polytomy shown in A.

relationships of portions of the genus have been reported (Jacobs et al., 1995). The present study extends the previous one to include all 12 recognized species of *Saguinus*.

## METHODS AND MATERIALS

### DNA extraction, amplification, and sequencing

Samples from ten species and subspecies of *Saguinus*, in addition to those represented in Jacobs et al. (1995), were obtained from a variety of sources (Table 1). Genomic DNA was extracted from the museum skin specimens (2–3 mm<sup>2</sup> of skin) using the tissue protocol of the QIAamp Tissue Kit (Qia-gen Inc., Chatsworth, CA). This same protocol was used to extract genomic DNA from an immortal cell line of *S. leucopus*.

Three segments of mitochondrial DNA (mtDNA) in the cytochrome *b* and D-loop

regions were amplified and sequenced for this analysis (Fig. 5). These regions have been shown previously to be phylogenetically informative for *Saguinus* (Jacobs et al., 1995). Because of the degraded nature of DNA extracted from museum skins, tamarin-specific primers were designed for this study to amplify smaller portions of the regions of interest. Primer sequences are listed in Table 2; all were used for both polymerase chain reaction (PCR) amplification and sequencing. Double-stranded PCR amplifications were run for 30 cycles under the following conditions: 92–94°C denaturation (35 sec), 50–55°C annealing (35 sec), and 70–72°C extension (2.5 min for the first cycle with an addition 4 sec for each ensuing cycle).

Because only a limited amount of DNA could be extracted from museum skins, 25 µl amplifications were first performed for these samples. DNA extracted from museum skins

TABLE 1. Sources for *Saguinus* samples used for this study<sup>1</sup>

Species	Tissue type	Source	Specimen ID
<i>S. bicolor bicolor</i>	Museum skin	R. Thorington	2053, 2074, 2075, 2076
	Extracted DNA	H. Schneider	1070
<i>S. bicolor martinsi</i>	Extracted DNA	H. Schneider	814
<i>S. bicolor ochraceus</i>	Museum skin	AMNH	94093, 94100
<i>S. fuscicollis lagonotus</i>	Frozen muscle	WU	none
	Museum skin	FMNH	60349
<i>S. fuscicollis fuscus</i>	Museum skin	FMNH	123377, 123378
<i>S. inustus</i>	Museum skin	AMNH	78596, 79415, 79418
<i>S. leucopus</i>	Immortal cell line	D. Evans	EBU
	Museum skin	USNM	216697, 216698
<i>S. midas niger</i>	Museum skin	AMNH	10159, 70166
<i>S. mystax pluto</i>	Museum skin	FMNH	134479
<i>S. tripartitus</i>	Museum skin	FMNH	57620
	Museum skin	AMNH	72098, 165934

<sup>1</sup> Sample sources for all species other than those listed here can be found in Jacobs et al. (1995). AMNH, American Museum of Natural History, New York; FMNH, Field Museum of Natural History, Chicago; USNM, National Museum of Natural History, Washington, DC; WRPFC, Wisconsin Regional Primate Research Center, Madison; WU, Washington University, Department of Anthropology, St. Louis.

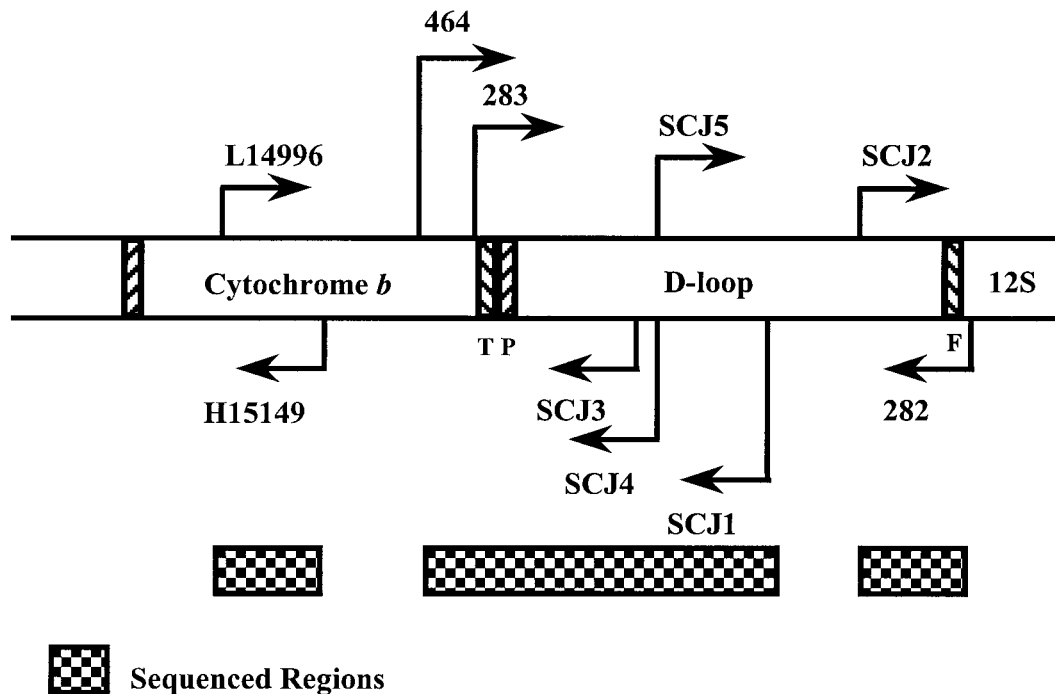


Fig. 5. Regions of mtDNA sequenced for phylogenetic analysis. The attachment sites for the primers listed in Table 2 are indicated by labeled arrows. Right arrows indicate light-strand primers, and left arrows indicate heavy-strand primers. F, phenylalanine transfer RNA gene (tRNA); P, proline tRNA; T, threonine tRNA.

has been found to contain degradation products and other contaminants that have an inhibitory effect on PCR amplifications. To enhance the reactions, we added 10 µg/µl bovine serum albumin (BSA) (Promega, Madison, WI) to the initial 25 µl reactions,

and the amount of TAQ DNA polymerase (Gibco, Inc., Grand Island, NY) in the initial amplifications was increased to twice the normal amount (Pääbo et al., 1988). The product was then purified on a low-melt agarose gel and reamplified in 100 µl reac-



TABLE 2. Primers used for PCR amplification and sequencing of the mtDNA<sup>1</sup>

Primer	Sequence (5' to 3')
282 (H) <sup>2</sup>	AAGGCTAGGACCAACCT
283 (L) <sup>2</sup>	TACACTGGTCTTGTAAC
464 (L) <sup>2</sup>	TGAATTGGAGGACAACCAGT
SCJ1 (H)	GAGCGAGAATACTAGTAGAAG
SCJ2 (L)	ACCCTTCAGAGAATAAACTTA
SCJ3 (L)	GTTAGTCATTACAGGGGATA
SCJ4 (L)	GCACTAATTACATAACCAA
SCJ5 (H)	TTGGTTATGTAATTAGTGC
H15149 (H) <sup>2</sup>	TGACTGTGGCACCTCAGAATGATATTGGCCTCA
L14996 (L) <sup>2</sup>	AGCCCCATCCAACATCTCTGCTTGATGAAA

<sup>1</sup> An (L) indicates a light-strand primer, and an (H) indicates a heavy-strand primer. Attachment sites for these primers are shown in Fig. 5.

<sup>2</sup> For references for these primers, see Jacobs et al., 1995; all others were designed for this study.

tions to obtain sufficient product for the sequencing reactions. Negative controls were run for all sets of PCR reactions to ensure the reactions were not contaminated with extraneous DNA. Any reactions containing product in the negative controls were discarded. Amplification products from the 100 µl reactions were purified on a 3.5% polyacrylamide gel in preparation for the sequencing reactions.

Double-stranded sequencing reactions were performed using either Sequenase version 2.0 (U.S. Biochemical, Cleveland, OH) (Hillis et al., 1996) or using a *fmol* cycle sequencing kit (Promega Corp., Madison, WI). Radiolabelled <sup>32</sup>P or <sup>35</sup>S (NEN, Boston, MA) was incorporated into the sequencing reactions, which were electrophoresed on a 6% polyacrylamide Long Ranger gel (FMC BioProducts, Rockland, ME). The regions sequenced included approximately 1,200 nucleotide bases, which includes more of the D-loop region than was previously reported (Jacobs et al., 1995).

### Phylogenetic analysis

Homologous sites of the mtDNA sequences were aligned manually and analyzed with Phylogenetic Analysis Using Parsimony (PAUP), version 3.1.1 (Swofford, 1993). Using *Callimico*, *Callithrix*, *Cebuella*, and *Leontopithecus* as the outgroup reference taxa, we used the heuristic search option (random addition of taxa, 20 replications) to find the most parsimonious phylogenetic reconstruction

for *Saguinus*. More alignable sequence data were obtained for *Saguinus* than for any of the outgroup taxa. Once the most parsimonious reconstruction was obtained for the tamarins using the outgroup taxa, the phylogenetic relationships among each of the two major clades within the genus were analyzed separately, each using the other clade as the outgroup. The purpose of the additional analyses was to take advantage of the additional data obtained for the *Saguinus* species and subspecies.

A branch-and-bound analysis was then performed on the data using the length of the most parsimonious reconstruction as an upper bound. The data were also subjected to a bootstrap analysis (Felsenstein, 1985b) using the heuristic search option with a random-addition sequence (three random-addition replications per bootstrap replication) for 200 bootstrap replications. The aforementioned analyses were performed on the entire data set including the other callitrichid genera and on the individual clades within *Saguinus*. Alternative hypotheses for the entire *Saguinus* phylogeny and for the *S. fuscicollis* subspecies were compared using a nonparametric Wilcoxon signed-ranks test (Templeton, 1983a,b; Felsenstein, 1985a). Branch lengths for the most parsimonious tree were estimated using the ACCTRAN and DELTRAN options of PAUP (Swofford, 1993). ACCTRAN resolves homoplasies preferentially as reversals, whereas DELTRAN favors parallelisms. Homoplasy is quantified using the consistency index and the homoplasy index.

### Geographic distributions

The current geographic distributions for the 12 tamarin species were obtained mainly from Hershkovitz (1977). Information from more recent censuses was incorporated as well (for a review see Rylands et al., 1993).

### RESULTS

Sequence data spanning approximately 1,200 bases in the cytochrome *b* and D-loop regions of the mtDNA were obtained for

*Saguinus* as well as representatives from *Callimico*, *Callithrix*, *Cebuella*, and *Leontopithecus*. The aligned sequence data can be found in the Appendix. For many of the museum skin specimens, the DNA was degraded, and only small fragments could be amplified and sequenced. Pairwise distances between the taxa (adjusted for missing data) are listed in Table 3.

An exact search of the aligned sequence data using *Callimico* as an outgroup yielded a single most parsimonious tree (Fig. 6). This tree is 1,325 steps long, with a consistency index of 0.543 and a homoplasy index of 0.457. The branch lengths were calculated with both the ACCTRAN and DELTRAN options of PAUP. Heuristic searches of the aligned sequence data using other callitrichid outgroups resulted in less resolution but were consistent with the tree in Figure 6.

As demonstrated before (Jacobs et al., 1995), *Saguinus* is a monophyletic taxon composed of two major clades: one containing *S. nigricollis*, all the *S. fuscicollis* subspecies, and *S. tripartitus*, and the other clade containing all remaining species. All species in this second clade have a 77 base deletion in the middle of the D-loop region compared to the *nigricollis/fuscicollis/tripartitus* clade. For simplicity, the clade containing *S. nigricollis*, *S. tripartitus*, and the *S. fuscicollis* subspecies will hereafter be known as the Small-bodied clade and the other major clade will be termed the Large-bodied clade, in reference to the relative body sizes of the species in the two clades.

The addition of *S. tripartitus* and *S. fuscicollis fuscus* to the analysis has revealed *S. fuscicollis* to be a paraphyletic taxon; *S. f. fuscus* is most closely related to *S. nigricollis*, and *S. tripartitus* is the sister taxon of *S. f. lagonotus*. However, with the exception of *S. fuscicollis*, all other species containing multiple subspecies are monophyletic. *Saguinus mystax* appears to form a monophyletic group with *S. labiatus* and *S. imperator*, a relationship that was not revealed with the previous, smaller data set (Jacobs et al., 1995). *Saguinus leucopus* is the sister taxon of *S. oedipus* and *S. geoffroyi*, which is not surprising given the close proximity of the

geographic ranges of these three species. That clade is the sister group to the clade containing *S. midas* and *S. bicolor*. *Saguinus inustus*, a species about which very little is known, appears to be the sister taxon to the *labiatus/imperator/mystax* clade.

The 50% majority-rule bootstrap analysis yielded the topology shown in Figure 7. Many of the nodes in this tree appear well resolved, as indicated by bootstrap values greater than 70. The bootstrap analysis supports *Saguinus* as a monophyletic taxon containing two major clades. Although the relationships within the Small-bodied clade are not all well resolved, *S. fuscicollis* still appears to be paraphyletic. The bootstrap analysis supports the conclusion that *S. mystax*, *S. midas*, and *S. bicolor* each forms monophyletic groups of populations. The structure of the clade containing *S. geoffroyi*, *S. oedipus*, *S. leucopus*, *S. midas*, and *S. bicolor* also is well supported. The deeper-level relationships within the second major clade lack resolution in this analysis.

Further phylogenetic analysis of the individual tamarin clades failed to yield more resolution. As can be seen in Figure 8A, the single most parsimonious reconstruction from an exact search of the sequence data for the Small-bodied clade using *S. m. mystax* as an outgroup has virtually the same structure as in Figure 6. The only differences are the relationships of *S. tripartitus* and *S. f. lagonotus* to the remainder of the clade. Although the 50% majority-rule bootstrap consensus for the single-clade analysis (Fig. 8B) reveals the same ambiguity in the basal portions of the clade as seen in the previous analysis (Fig. 7), there is great support for the grouping of *S. f. fuscus* with *S. nigricollis*. An exact search of the sequence data for the Large-bodied clade (using *S. f. melanoleucus* and *S. nigricollis* as outgroups) yielded the same topology as before (Fig. 9A), and a bootstrap analysis of the same data (Fig. 9B) again failed to resolve the deeper relationships within the clade.

The molecular tree (Fig. 6) was compared to the hypothetical tree based on Ferrari (1993a) (Fig. 4A) using a Wilcoxon signed-ranks test (Templeton 1983a,b; Felsenstein,



TABLE 3. Pairwise comparisons of mtDNA sequences among the taxa used in the study<sup>1</sup>

Taxon	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
1. <i>Callimico sp.</i>	0.149	0.148	0.157	0.151	0.163	0.151	0.152	0.157	0.170	0.139	0.154	0.130	0.146	0.157	0.152	0.144	0.114	0.170	0.162	0.178	0.177	0.184	0.184	0.174	0.205	0.117
2. <i>Cebuella sp.</i>		0.174	0.109	0.182	0.188	0.174	0.178	0.182	0.193	0.177	0.190	0.164	0.183	0.190	0.179	0.168	0.151	0.194	0.194	0.190	0.183	0.211	0.196	0.190	0.245	0.234
3. <i>Leontopithecus sp.</i>			0.167	0.177	0.168	0.174	0.174	0.170	0.172	0.168	0.184	0.150	0.174	0.190	0.178	0.170	0.161	0.199	0.197	0.204	0.179	0.215	0.192	0.182	0.206	0.147
4. <i>Callithrix sp.</i>				0.185	0.189	0.172	0.179	0.187	0.189	0.166	0.201	0.150	0.182	0.204	0.200	0.164	0.167	0.215	0.215	0.218	0.182	0.219	0.198	0.204	0.225	0.248
5. <i>S. f. fuscicollis</i>					0.052	0.046	0.070	0.066	0.065	0.053	0.090	0.057	0.086	0.183	0.167	0.151	0.134	0.188	0.184	0.206	0.169	0.200	0.204	0.191	0.185	0.234
6. <i>S. f. nigrifrons</i>						0.052	0.075	0.064	0.074	0.058	0.083	0.064	0.086	0.181	0.171	0.151	0.149	0.201	0.195	0.207	0.171	0.200	0.204	0.197	0.202	0.221
7. <i>S. f. illigeri</i>							0.025	0.049	0.061	0.056	0.046	0.051	0.053	0.140	0.128	0.134	0.135	0.160	0.166	0.173	0.173	0.203	0.178	0.169	0.204	0.164
8. <i>S. f. leucogenys</i>								0.072	0.075	0.057	0.063	0.038	0.078	0.175	0.153	0.133	0.128	0.199	0.189	0.212	0.160	0.179	0.208	0.193	0.202	0.251
9. <i>S. f. melanoleucus</i>									0.050	0.060	0.091	0.056	0.098	0.179	0.167	0.153	0.138	0.198	0.192	0.206	0.166	0.193	0.201	0.185	0.187	0.242
10. <i>S. f. weddelli</i>										0.061	0.092	0.057	0.101	0.186	0.167	0.150	0.136	0.203	0.194	0.210	0.173	0.197	0.204	0.193	0.190	0.222
11. <i>S. f. fuscus</i>											0.052	0.045	0.024	0.144	0.123	0.135	0.125	0.172	0.164	0.152	0.167	0.208	0.170	0.170	0.197	0.168
12. <i>S. f. lagonotus</i>												0.035	0.094	0.178	0.158	0.155	0.160	0.203	0.194	0.206	0.177	0.195	0.198	0.186	0.208	0.232
13. <i>S. tripartitus</i>													0.051	0.138	0.122	0.127	0.126	0.158	0.157	0.142	0.150	0.153	0.157	0.154	0.181	0.194
14. <i>S. nigricollis</i>														0.181	0.161	0.136	0.121	0.204	0.195	0.230	0.175	0.195	0.221	0.206	0.181	0.248
15. <i>S. labiatus</i>															0.088	0.089	0.102	0.138	0.148	0.155	0.147	0.165	0.152	0.153	0.173	0.144
16. <i>S. imperator</i>																0.096	0.116	0.132	0.132	0.144	0.143	0.163	0.139	0.131	0.159	0.105
17. <i>S. mystax mystax</i>																	0.021	0.137	0.140	0.137	0.154	0.167	0.169	0.164	0.175	0.091
18. <i>S. mystax pluto</i>																		0.134	0.129	0.139	0.151	0.113	0.157	0.158	0.137	0.112
19. <i>S. geoffroyi</i>																			0.049	0.105	0.142	0.165	0.141	0.137	0.169	0.176
20. <i>S. oedipus</i>																				0.107	0.129	0.172	0.142	0.132	0.171	0.174
21. <i>S. leucopus</i>																					0.109	0.100	0.122	0.127	0.116	0.135
22. <i>S. midas midas</i>																						0.034	0.095	0.091	0.110	0.186
23. <i>S. midas niger</i>																							0.121	0.110	0.121	0.243
24. <i>S. bicolor bicolor</i>																								0.041	0.034	0.150
25. <i>S. bicolor martinsi</i>																									0.017	0.143
26. <i>S. bicolor ochraceus</i>																										0.211
27. <i>S. inustus</i>																										

<sup>1</sup> Distances were calculated using PAUP version 3.1.1 and have been adjusted for missing data. *S.* = *Saguinus*; *f.* = *fuscicollis*.

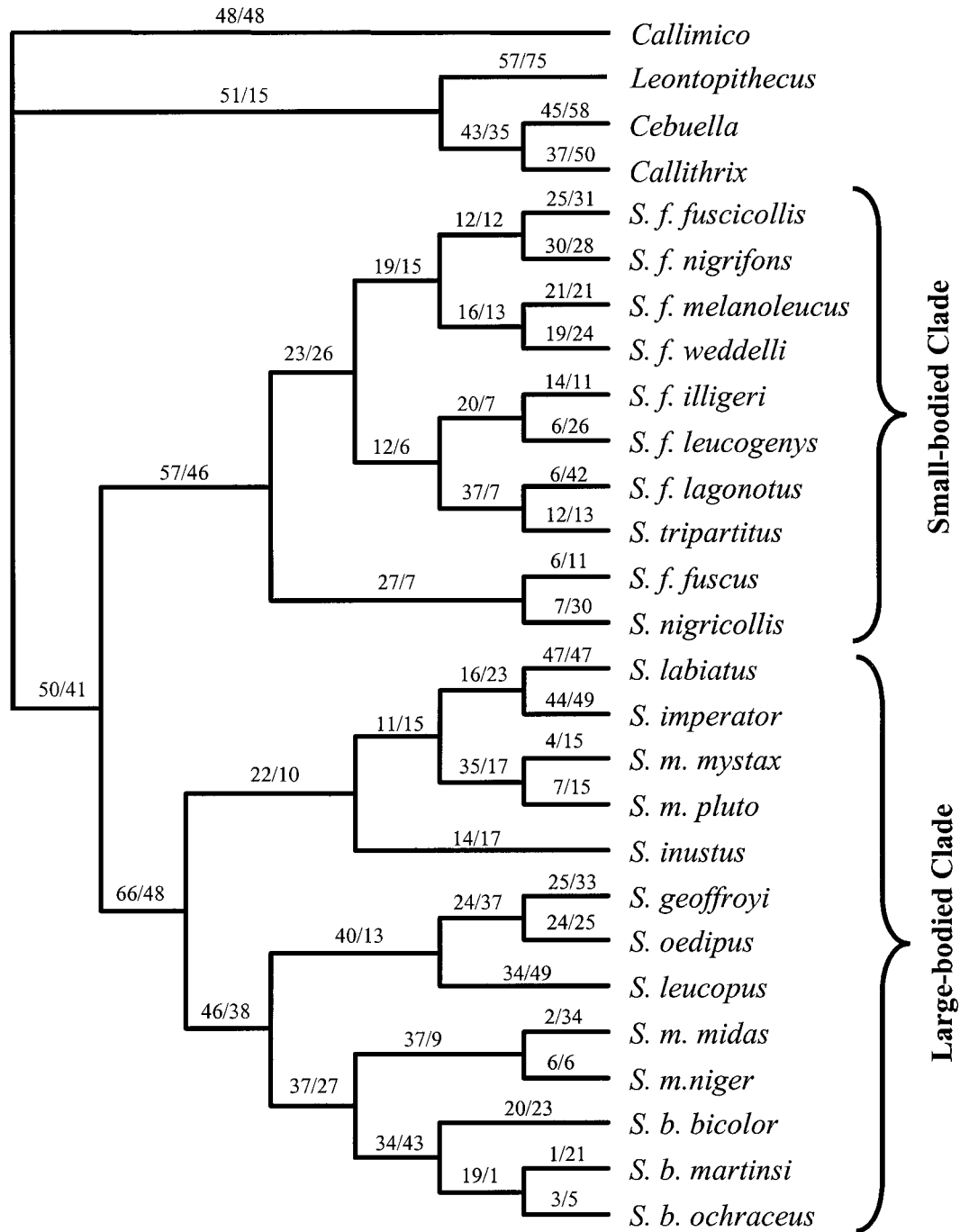


Fig. 6. Single most parsimonious tree resulting from a heuristic search (random additions option, ten replications) of the sequence data using *Callimico* as the outgroup reference taxon. The numbers above the branches are the ACCTRAN/DELTRAN branch lengths. The total number of changes on the tree is 1325. The consistency index is 0.543, and the homoplasy index is 0.457.

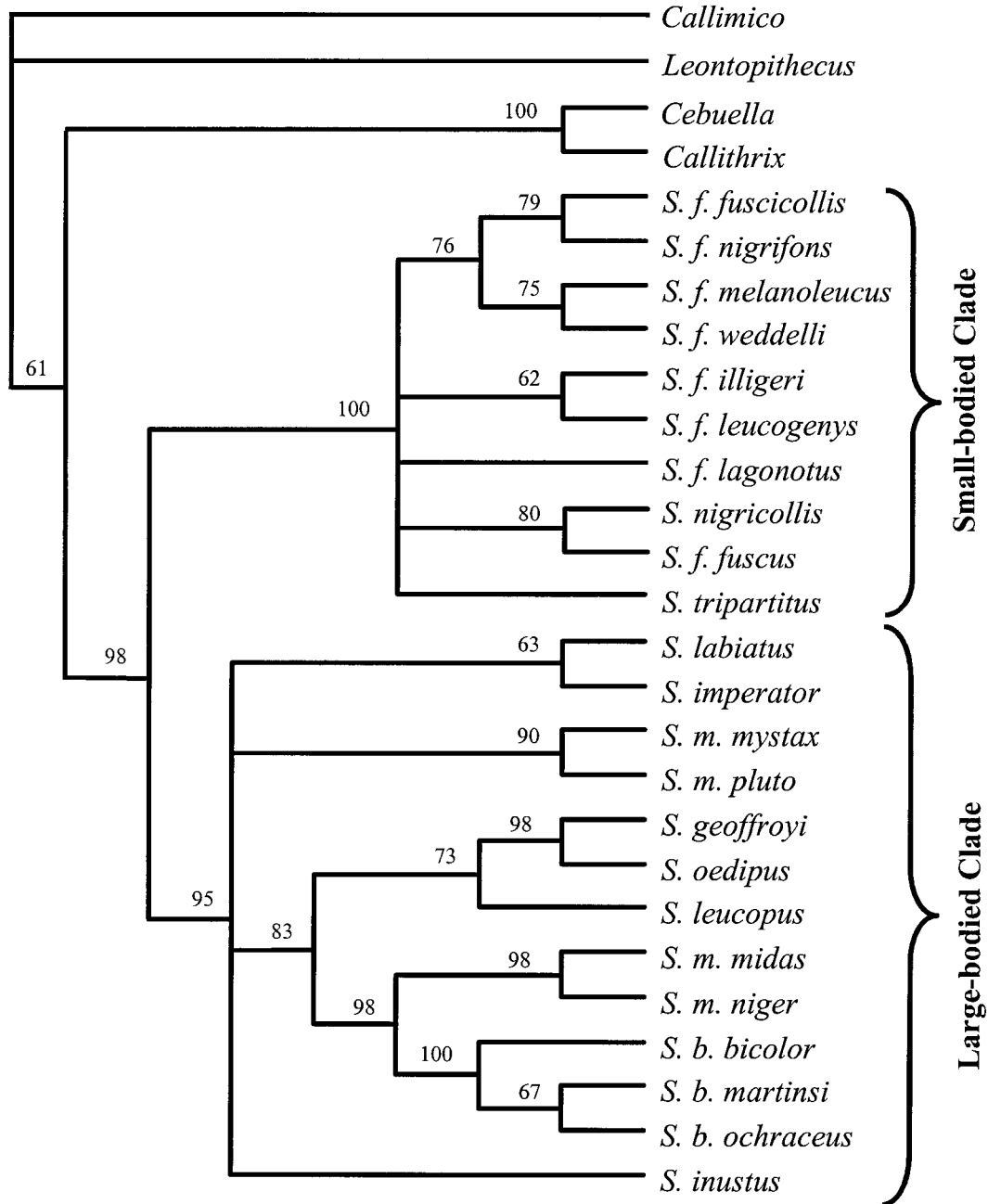


Fig. 7. The 50% majority-rule bootstrap consensus of the mtDNA sequence data using *Callimico* as the outgroup. Bootstrap values obtained from 200 replications (three random additions per replication) are shown above the branches.

1985a). Before comparing the two trees, we rearranged the polytomy in Figure 4A to produce the most parsimonious bifurcating clade consistent with the polytomy (Fig. 4B).

Ferrari (1993a) made no mention of the relationships among any of the subspecies groups, so only *S. f. fuscicollis* was retained in both trees as a representative of the *S.*

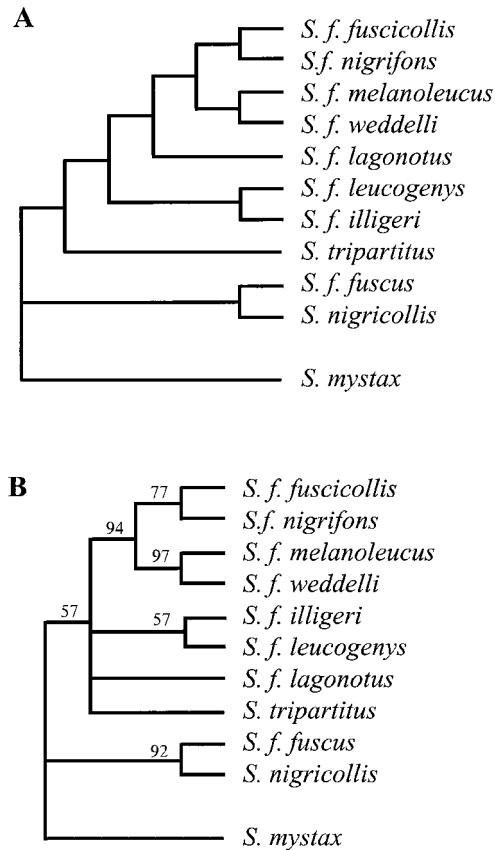


Fig. 8. **A:** The single most parsimonious tree resulting from an exact search of the mtDNA sequence data for the Small-bodied clade using *S. mystax mystax* as an outgroup (tree length = 412 steps, C.I. = 0.771, H.I. = 0.229). **B:** The 50% majority-rule bootstrap consensus of the same data set. Bootstrap values obtained from 200 replications (three random additions per replication) are shown above the branches.

*fuscicollis* subspecies. In addition, only *S. b. bicolor* and *S. b. martinsi* were used as representatives of the *S. bicolor* subspecies group to yield a bifurcating *S. bicolor* clade. *Saguinus bicolor ochraceus* was eliminated from both trees in this particular analysis because the least amount of sequence was collected for this subspecies. The hypothetical phylogeny based on Ferrari (1993a) was significantly less parsimonious than the molecular tree ( $N = 87$ ,  $T = 560$ ,  $P < 0.001$ , two-tailed test).

The molecular tree (Fig. 6) was compared also to Hershkovitz's (1977) hypothetical

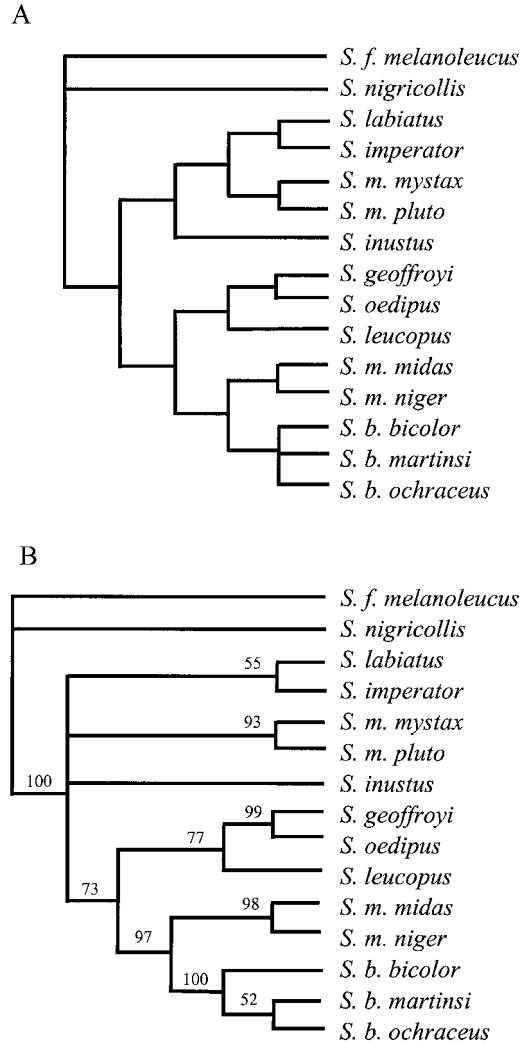


Fig. 9. **A:** The strict consensus of the three equally most parsimonious trees resulting from an exact search of the mtDNA sequence data for the Large-bodied clade of *Saguinus* using *S. fuscicollis melanoleucus* and *S. nigricollis* as outgroups (tree length = 751, C.I. = 0.679, H.I. = 0.321). **B:** The 50% majority-rule bootstrap consensus of the same data set. Bootstrap values obtained from 200 replications (three random additions per replication) are shown above the branches.

phylogeny (Fig. 3A) using the relationships among the *S. fuscicollis* subspecies depicted in Figure 3B. Hershkovitz also made specific predictions concerning the relationships among the *S. bicolor* subspecies that were used to create a bifurcating structure for that clade in the hypothetical phylogeny.

Hershkovitz's (1977) hypothetical phylogeny was significantly less parsimonious than the molecular tree ( $N = 83$ ,  $T = 975$ ,  $P < 0.001$ , two-tailed test). The Small-bodied clade of the molecular tree alone was compared to the hypothetical tree in Figure 3B. The phylogenetic relationships among *S. nigricollis* and the *S. fuscicollis* subspecies hypothesized by Hershkovitz (1977) were significantly less parsimonious than the topology of the Small-bodied clade of the molecular tree ( $N = 38$ ,  $T = 211$ ,  $P = 0.02$ , two-tailed test). Also, the Small-bodied clade (Fig. 8A) was rearranged to reflect a monophyletic *S. fuscicollis* clade by grouping *S. f. fuscus* with the other *S. fuscicollis* subspecies. This rearrangement was significantly less parsimonious ( $N = 15$ ,  $T = 24$ ,  $P = 0.04$ , two-tailed test).

Hershkovitz postulated that the northern bare-face tamarins (*S. oedipus*, *S. leucopus*, and *S. geoffroyi*) arose from ancestral *S. inustus*. A topology grouping *S. inustus* basal to the clade of the three northern bare-face tamarins was compared with the molecular tree. This rearrangement of the Large-bodied clade was not significantly less parsimonious than the molecular tree ( $N = 14$ ,  $T = 30$ ,  $P > 0.1$ , two-tailed test).

## DISCUSSION

### Tamarin phylogeny

The molecular phylogenetic relationships among some of the tamarin species have been reported previously (Jacobs et al., 1995), but the present analysis includes all 12 species and nearly all of the subspecies. The present analysis is congruent with the findings of Jacobs et al. (1995). *Saguinus* is a monophyletic taxon composed of two major clades: the Small-bodied clade containing *S. nigricollis*, *S. tripartitus*, and *S. fuscicollis* and the Large-bodied clade, which contains the remainder of the species. These results agree with Garber's (1992) division of *Saguinus* into two major clades (*S. fuscicollis* and *S. nigricollis* in one clade and all others in a second clade) based on feeding adaptations related to body size. Whether Garber (1992) considers *S. tripartitus* as a subspecies of *S.*

*fuscicollis* and therefore a member of the same clade is not explicitly stated.

Three more species are now included in the Large-bodied clade than in the Jacobs et al. (1995) study: *S. leucopus*, *S. bicolor*, and *S. inustus*. Hershkovitz (1977) proposed that *S. leucopus* was most closely related to *S. oedipus* and *S. geoffroyi*. His hypothesis is supported by the molecular data (Fig. 6) and is not surprising given the geographic proximity these three species and their geographic isolation. Cladistic and morphometric analyses of craniofacial features also group these three species (Natori and Hanihara, 1988; Moore and Cheverud, 1992), although Moore and Cheverud (1992) found *S. oedipus* to be more similar morphologically to *S. leucopus* than to *S. geoffroyi*.

Based on the sequence data, the *S. bicolor* subspecies form a monophyletic group and are the sister taxon to *S. midas*. Hershkovitz (1977) hypothesized this same relationship based on coat color and the adjacent geographic ranges of these taxa north of the Amazon (Fig. 1A). The sister-group relationship of *S. bicolor* and *S. midas* also agrees with cladistic analyses of morphological features (Natori and Hanihara, 1988; Natori, 1988) and with ecological evidence (Ferrari, 1993a).

In the most parsimonious phylogenetic reconstruction (Fig. 6), *S. inustus* is a sister taxon to a group containing *S. mystax*, *S. labiatus*, and *S. imperator*. Jacobs et al. (1995) found a monophyletic group composed of *S. labiatus*, *S. imperator*, and *S. mystax*, but a bootstrap analysis of the relationships among this clade lacked sufficient resolution to make any firm conclusions. The grouping of these three species together with *S. inustus* is not well supported by bootstrap analysis (Fig. 7). The failure of additional sequence data for *S. labiatus*, *S. imperator*, and *S. mystax* to resolve the relationships among these three species suggests that a rapid radiation may have occurred amongst these species that would not be recoverable using parsimony analysis. The lack of resolution for the phylogenetic position of *S. inustus* could be attributed to the same phenomenon or could be due to the relatively small amount of sequence data

generated for *S. inustus* (Appendix) compared to the other species in the analysis. Hershkovitz (1977) proposed that *S. inustus* was most closely related to the northern bare-face tamarins, *S. oedipus*, *S. leucopus*, and *S. geoffroyi*, and rearranging the phylogenetic tree to reflect this relationship is not significantly less parsimonious than the molecular tree in Figure 6. Ferrari (1993a) grouped *S. inustus* with *S. bicolor* and *S. midas*, although this decision was based partially on the lack of evidence linking *S. inustus* to any other tamarins. Cladistic analysis of craniodental features lacked resolution in the relationship of *S. inustus* to the other tamarins (Natori, 1988). The lack of consensus among data sets indicates the need for more information about this little-known species.

The phylogenetic relationships among members of the Small-bodied clade, although not all completely well resolved, do make sense geographically (Fig. 1). The molecular data indicate that *S. f. fuscicollis* and *S. f. nigrifrons* are sister taxa, and the ranges of these two subspecies are separated only by the Rio Javari (Hershkovitz, 1977). The ranges of *S. f. melanoleucus* and *S. f. weddelli* are geographically close as well, which agrees with the grouping of these two as sister taxa. Cheverud and Moore (1990) also found that the facial morphology of *S. f. melanoleucus* and *S. f. weddelli* was quite similar. Together, all four subspecies form a well supported clade that ranges from the western bank of the Rio Madeira/Rio Marmore to the eastern side of the Rio Ucayali. These results are supported by a cluster analysis of morphological distances that grouped *S. f. nigrifrons* and *S. f. weddelli* (Moore and Cheverud, 1992), although the other two species in the clade, *S. f. melanoleucus* and *S. f. fuscicollis*, were not included in the morphological analysis. Had *S. f. avilapiresi* been included in the present study, it seems likely that it would have been related to this clade, given that the geographic range of this subspecies is within the bounds of the clade.

Although the support for *S. f. illigeri* and *S. f. leucogenys* as sister taxa is relatively

weak (Fig. 7), their geographic ranges do adjoin on opposite banks of the Rio Hualaga. However, a systematic study of cranial morphology failed to yield a close relationship between the two subspecies (Moore and Cheverud, 1992). The lack of resolution in the more basal portions of the *S. fuscicollis* group could be due to lack of sufficient variability in the regions of mtDNA that were sequenced. However, the D-loop region of the mtDNA is the most variable in mammals (Avise et al., 1987) and should yield the greatest number of informative sites. An alternative explanation is that a rapid initial radiation of the *S. fuscicollis* group occurred.

In the Jacobs et al. (1995) study, *S. fuscicollis* was a monophyletic species. However, the inclusion of *S. f. fuscus* and *S. tripartitus* in the present study shows *S. fuscicollis* to be a paraphyletic species. As can be seen in Figure 6, *S. f. fuscus* groups with *S. nigrifrons* rather than the other *S. fuscicollis* subspecies, a relationship that is well supported by the bootstrap analysis (Fig. 7). This relationship is again revealed by the single most parsimonious tree and the bootstrap consensus resulting from the single-clade analysis as shown in Figure 8. In addition, grouping *S. f. fuscus* with the other *S. fuscicollis* subspecies is significantly less parsimonious than the molecular tree shown in Figure 8A. Based on the degree of divergence in facial morphology of *S. f. fuscus* from the other *S. fuscicollis* subspecies, Moore and Cheverud (1992) have suggested that this subspecies might deserve species status. The present results support that suggestion, and a change in the taxonomic status of *S. f. fuscus* to *S. fuscus* would maintain the monophyly of *S. fuscicollis*. *Saguinus tripartitus* also disrupts the monophyly of *S. fuscicollis* because the most parsimonious phylogenetic reconstruction links it with *S. f. lagonotus* (Fig. 6). However, this relationship is not well supported by the bootstrap analysis (Fig. 7), nor is it well supported in the single clade analysis (Fig. 8). Hershkovitz's (1977) original taxonomy included *S. tripartitus* as a subspecies of *S. fuscicollis*. Subsequent studies of the geographic range of this taxon



have shown that this group should have species status (Thorington, 1988; Albuja, 1994), and this revised classification for *S. tripartitus* is generally accepted. Because of the ambiguity of the phylogenetic relationship of this species to the remainder of the *S. fuscicollis* clade, *S. fuscicollis* could still be considered tentatively monophyletic provided the taxonomy of *S. f. fuscus* is revised.

### Historical biogeography

Ferrari's (1993a) dispersal scheme for tamarins was derived from a phylogenetic hypothesis based on ecological factors related to body size. However, the phylogenetic relationships upon which his dispersal scheme is based are significantly less parsimonious than the phylogeny inferred from the mtDNA sequence data. Phyletic dwarfism was originally proposed to account for several apparently derived morphological features shared by extant callitrichids. These features include small body size, loss of the third molar, reproductive twinning, and claws instead of nails (Ford, 1980; Leutenegger, 1980). The theory did not espouse body size as a phylogenetic character. In the absence of good fossil evidence, dwarfing was hypothesized as a single *rapid* event that occurred in the ancestral callitrichid lineage. In fact, a test of the phyletic dwarfism hypothesis based on dental metric data failed to support certain morphological predictions of the hypothesis (Plavcan and Gomez, 1993a,b). Therefore, the dispersal routes for *Saguinus* derived from Ferrari's (1993a) phylogenetic hypothesis are unlikely.

The dispersal scheme of Hershkovitz (1977) for *Saguinus* also seems improbable, since his phylogenetic hypothesis based on the theory of metachromism also was significantly less parsimonious than the molecular phylogeny. Jacobs et al. (1995) obtained results similar to the ones presented here with a partial tamarin phylogeny. Hershkovitz (1968, 1977) proposed the theory of metachromism to be a phylogenetic phenomenon. However, others have cautioned against using coat color as a phylogenetic character due to the likelihood of parallelisms occurring among lineages (Shedd and

Macedonia, 1991; Jacobs et al., 1995). Jacobs et al. (1995) demonstrated coat color to be a poor character for phylogenetic analysis.

Given the phylogenetic relationships among tamarins inferred from the mtDNA sequence data, a plausible version of the historical dispersal routes for tamarins is shown in Figure 10. The most basal division among the ancestral tamarins is a bifurcation between the Small-bodied clade and the Large-bodied clade. If we take the region of highest diversity as the most likely area of origin for the tamarins, the ancestral *Saguinus* would have arisen somewhere south of the Amazon and west of the Rio Madeira. This scenario is in agreement with Hershkovitz (1977). The split between the ancestors of the two clades could have occurred by a vicariance event or by migration. A subsequent dispersal of *S. fuscicollis* in a southeasterly direction would have brought them back into sympatry with the southern species of the Large-bodied clade. Two waves of dispersal north across the Amazon would account for the distributions of *S. inustus* to the west and *S. bicolor* and *S. midas* to the east. A monophyletic grouping of *S. bicolor*, *S. midas*, and the northern bareface tamarins indicates that the ancestors of the latter group arrived in northern Colombia and Panama from the northern regions of South America rather than the southern origins proposed by Hershkovitz (1977). This dispersal hypothesis reflects the most parsimonious phylogenetic relationships among *Saguinus*, as shown in Figure 6.

The phylogenetic relationships among *S. fuscicollis* suggest that this group radiated in a southeasterly direction instead of the southwestern direction suggested by Hershkovitz (1977) (Fig. 10B). Peres et al. (1996) have shown that hybridization (and hence dispersal) occurs at the headwaters of the Rio Jurua, which separates the geographic ranges of *S. f. fuscicollis* and *S. f. melanoleucus*. Therefore, the dispersal route for *S. fuscicollis* depicted in Figure 10B is conceivable, given that such a dispersal could have

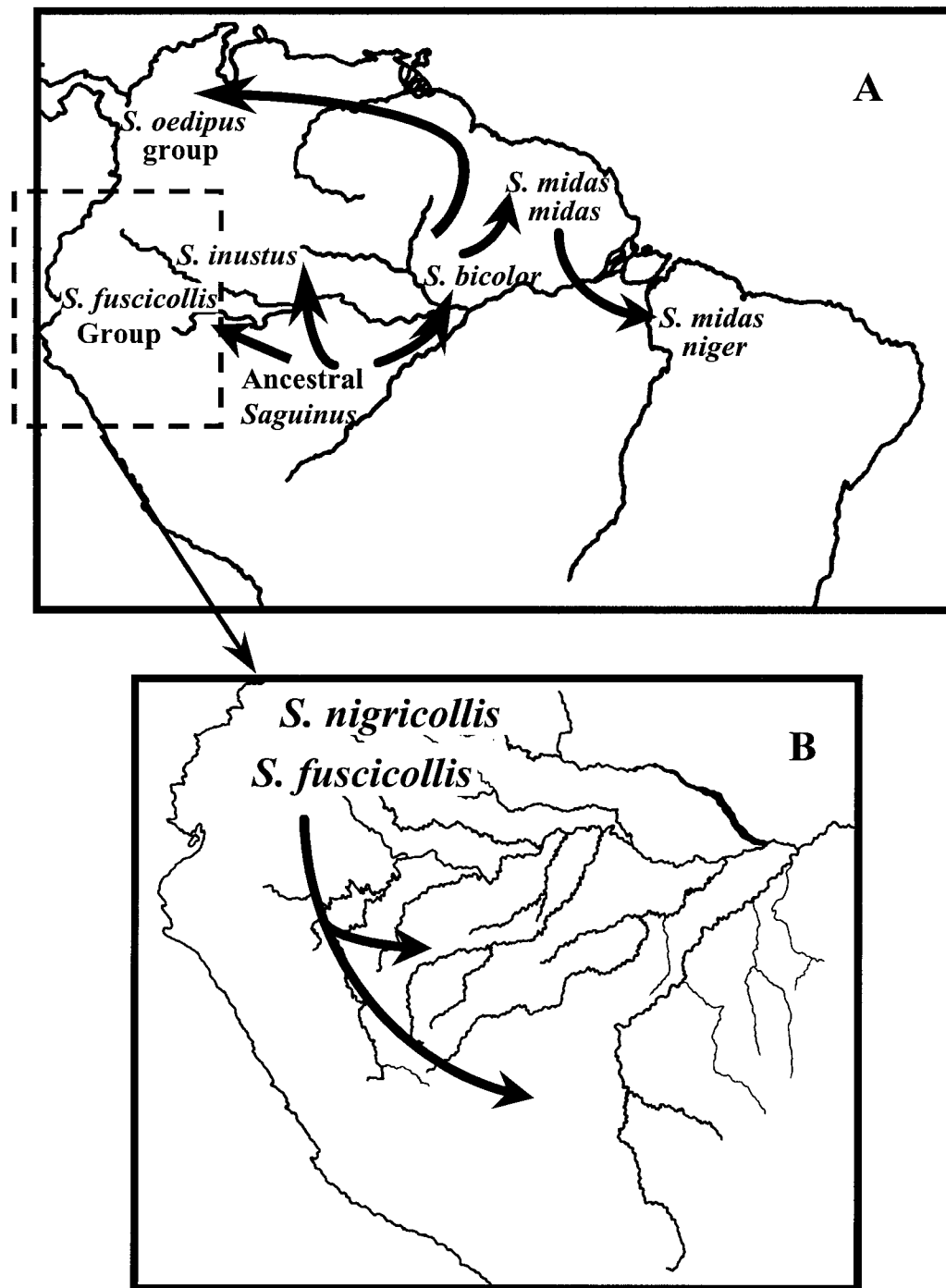


Fig. 10. Proposed historical dispersal for *Saguinus* **A**: and the *S. fuscicollis* **B**: subspecies based on the molecular phylogenetic evidence.

occurred around the headwaters of the various rivers separating the subspecies.

Dating the dispersal events that led to the geographic distribution of extant tamarins is difficult. The paucity of primate fossil remains from the Neotropics allows for only the roughest estimate for the divergence time of *Saguinus* from the other callitrichids. The oldest known South American primate fossil, *Branisella*, was recovered from late Oligocene deposits in Bolivia (Hoffstetter, 1969; Rosenberger, 1981b; Wolff, 1984). These remains place early primates in South America approximately 25 million years ago (Ma). More recent specimens that appear to be more closely related to extant callitrichines than *Branisella* have been unearthed from the La Victoria Formation in Colombia. Remains of a giant tamarin, *Lagonimico conclucatus*, have been dated to the middle Miocene, approximately 13.5 Ma. The original fossil, described by Kay (1994), appears to be a sister taxon to living callitrichids (callitrichines) rather than a direct ancestor. From the fossil evidence, therefore, we can estimate the age of the genus *Saguinus* as possibly 25 Ma but more likely closer to 13.5 Ma. Either way, divergence of *Saguinus* from the other callitrichids is clearly pre-Pleistocene.

Of course, the best way to test the dispersal hypothesis set forth in this study is to demonstrate that the pattern also holds true for other organisms similar to *Saguinus* in site of origin and physiogeographic features perceived as barriers to dispersal. *Saimiri* (squirrel monkeys) is another primate genus with a geographic distribution similar to that of tamarins. Squirrel monkeys are found in secondary and riverine forest throughout the Amazon basin, with a small disjunct population of *Saimiri oerstedii* located in Costa Rica (HersHKovitz, 1984). These primates are larger in body size than tamarins, but their geographic ranges, too, are limited by riverine barriers, although to a lesser extent than tamarins (Ayres and Clutton-Brock, 1992; S. Boinski, personal communication). Preliminary data collected for the Costa Rican *Saimiri* species and two species of South American squirrel monkeys indi-

cate a similar geographic pattern of phylogenetic relationships as *Saguinus* (Lepp et al., 1997). However, more extensive geographic sampling from *Saimiri* is needed before any definitive conclusions can be drawn.

## CONCLUSIONS

Within *Saguinus*, there are two major clades: the Small-bodied clade composed of *S. fuscicollis*, *S. tripartitus*, and *S. nigricollis* and the Large-bodied clade that contains the remainder of the species. A previous review of the taxonomy of *S. fuscicollis* subspecies elevated *S. f. tripartitus* to species status (Thorington, 1988), yet under the current taxonomy *S. fuscicollis* is still a paraphyletic taxon. Revision of the taxonomic status of *S. f. fuscus* from subspecies to species, *S. fuscus*, would maintain monophyly of *S. fuscicollis*. Such a revision is supported by morphological evidence (Moore and Cheverud, 1992) as well as the molecular evidence.

The molecular evidence suggests a different historical dispersal for tamarins than previously hypothesized (HersHKovitz, 1977; Ferrari, 1993a). The phylogenetic relationships among *Saguinus* suggest that tamarins dispersed in two major waves from an origin south of the Amazon and west of the Rio Madeira: one in a western direction leading to the distributions of the small-bodied tamarin clade and one in a northeastern and then western direction resulting in the distributions of *S. bicolor*, *S. midas*, and the northern bareface tamarins.

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# APPENDIX: Alignment of the sequence data used in the parsimony analysis

	Cytochrome b	100
<i>C.goeldii</i>	TTT TAGGTACCTGCCTAATCATTCAAATCACCACAGGACTATTCTAGCCATACA?TACACATCAGACACC??ACCGCCTTCTCCTCAGT?GCCCA?AT	
<i>C.jacchus</i>	.....T...?..T...????T...C.....A.....C.....??..?..?CT..??T...T.....T...T..	
<i>C.pygmaea</i>	??C.....?.....?.....C.....C.....A.....C?.....????????	
<i>L.rosalia</i>	.....T?T?.....T.....T.....C.....C.....A.....C.....CT.....TTCC.....T.....A.....C..	
<i>S.b.bicolor</i>	?????????????????????????????.....C.....C.....C.....C.....T????T.....T.....C.....T..	
<i>S.b.martinsi</i>	..C.....??T.....C.....C.....C.....C.....TACC.....T.....T.....C.....C..	
<i>S.b.ochraceus</i>	??	
<i>S.f.fuscicollis</i>	??	
<i>S.f.fuscus</i>	.CC.....C.....T.....T.....C.....T.....?.....T.....C.....C.....C.....T.....GCC.....T.....C.....C..	
<i>S.f.illigeri</i>	??????????????????????????G.T.A.....C.....C.....C.....G.....TGCC.....T.....A.....C..	
<i>S.f.lagonotus</i>	.CC.....??T.....T?.....T.....C.....G.....A.....T.....C.....C.....C.....TGCC.....T.....A.....C..	
<i>S.f.leucogenys</i>	??C.....?.....C.....G.....TGCC.....T.....A.....C..	
<i>S.f.melanoleucus</i>	C.C.....T.....T.....G.T.A.....T.....C.....C.....C.....TGCC.....T.....A.....C..	
<i>S.f.nigrifons</i>	??????????????????T?C.T.T.A.....?T.....C.....C.....C.....??TGCC.....T.....T.....?.....?.....C..	
<i>S.f.weddelli</i>	????????T.???.....T.....?..T.....?..A.....T?.....C.....T.....C.....C.....TACC.....T.....A.....C..	
<i>S.geoffroyi</i>	..C.....T.....A.....C.....CT.....AT.....G.....C.....C.....TGCC.....T.....C.....T.....C..	
<i>S.imperator</i>	.....G.....T.....T.....GCC.....A.....C..	
<i>S.inustus</i>	??	
<i>S.labiatus</i>	..C.....T.....?.....T.....C.....C.....C.....G.G.....TACT.....A.....C..	
<i>S.leucopus</i>	????????????????????????????????????CT..C.C.....C.....C.....TACT.....T.....T?.....T.....C..	
<i>S.m.midas</i>	.....T.....G.T.....C.....C.....C.....C.....TACC.....T.....T.....C.....T..	
<i>S.m.niger</i>	??	
<i>S.m.mystax</i>	??????????T..T?.....T.....T.....C.....C.....T.....GC.....C.....?.....?.....T.....C..	
<i>S.m.pluto</i>	..C.....C.T.....TT.....T.....T.....C.....C.....C.....C.....TTT.....C.....C..	
<i>S.nigricollis</i>	??	
<i>S.oedipus</i>	..C.....T.....A.....C.....CT.....AT.....G.....T.....GCC.....T.....C.....T.....C..	
<i>S.tripartitus</i>	.CC.....C.T.....T?.....T.....C.....T.....G.....T.....C.....C.....T.....TGCC.....T.....A.....C..	
		200
<i>C.goeldii</i>	CACTCGAGATGTTAACTACGGATGAATAATCCGTTACTTACATGCTAATGGTGCATCCATAITTTTCATCTGCCTCTT?CTCCACATTGGCCGAGGCTA	
<i>C.jacchus</i>	..C.....C.....T.....C.....C.....C.....C.....C.....C.....T.....C.....T.....CAC.?.....T..	
<i>C.pygmaea</i>	.....C.....C.....T.....C.....T.....A.....T.....C.....C.....C.....C.....T.....T.....T.....	
<i>L.rosalia</i>	T.....?.....T.....??????T.....T.....C.....C.....C.....C.....T.....C.....?.....A.....	
<i>S.b.bicolor</i>	..C.....?C.....A.....C.....C.....C.....C.....C.....AGC.....T?G.....C.....A.....T.....T.....G	
<i>S.b.martinsi</i>	..C.....C.....A.....C.....G.....A.....TC.G.....C.....C.....C.....G.....T?G.....C.....A.....T.....T.....G	
<i>S.b.ochraceus</i>	??	
<i>S.f.fuscicollis</i>	.....C.....A.....T.....C.....G.....C.....C.....C.....C.....?.....?.....G.....C.....T.....C.....T.....	
<i>S.f.fuscus</i>	..C.....C.....A.....T.....T.....C.....C.....C.....C.....C.....C.....T.....A.....C.....T.....C.....T.....G	
<i>S.f.illigeri</i>	..C.....C.....A.....T.....T.....C.....C.....C.....C.....C.....C.....T.....G.....C.....T.....C.....T.....A.G	
<i>S.f.lagonotus</i>	..C.....C.....A.....T.....T.....C.....C.....G.....C.....C.....C.....G.....T.....G.....C.....T.....C.....T.....T.G	
<i>S.f.leucogenys</i>	?.....C.....C.....A.....T.....T.....C.....C.....C.....C.....C.....C.....T.....G.....C.....T.....C.....T.....A.G	
<i>S.f.melanoleucus</i>	..C.....C.....A.....?.....T.....C.....?.....?.....C.....C.....C.....C.....T.....G.....C.....T.....C.....T.....G	
<i>S.f.nigrifons</i>	.....C.....C.....A.....T.....C.....C.....C.....C.....C.....C.....A.....T.....G.....T.....T.....C.....T.....G	
<i>S.f.weddelli</i>	..C.....C.....A.....T.....C.....C.....C.....C.....C.....C.....T.....G.....C.....T.....C.....T.....G	
<i>S.geoffroyi</i>	T.....C.....C.....A.....T.....C.....G.....C.....C.....C.....C.....C.....?.....TA.....A.....C.....A.....T.....C.....T.....	
<i>S.imperator</i>	T.....T.....A.....T.....T.....C.....C.....C.....C.....C.....C.....C.....T.....A.....C.....G.....T.....T.....TT.G	
<i>S.inustus</i>	??	
<i>S.labiatus</i>	T.....C.....C.....A.....T.....T.....??????C.....C.....C.....C.....C.....T.....C.....TT.....A.....T.....A.....T.....TT.G	
<i>S.leucopus</i>	T.....C.....C.....A.....T.....T.....T.....C.....C.....C.....C.....C.....C.....?.....TA.....A.....?T.....A.....T.....C.....T.....?	
<i>S.m.midas</i>	.....C.....A.....T.....T.....C.....T.....A.....T?.....C.....C.....C.....C.....??????????????????G.....C.....A.....T.....C.....T.....	
<i>S.m.niger</i>	??	
<i>S.m.mystax</i>	T.....CT.....C.....C.....T.....C.....C.....C.....C.....C.....C.....C.....C.....A.....C.....CA.....	
<i>S.m.pluto</i>	T.....CT.....C.....C.....C.....C.....C.....C.....C.....C.....C.....C.....A.....C.....C.....?	
<i>S.nigricollis</i>	..C.....C.....C.....A.....T.....T.....C.....C.....C.....C.....C.....C.....T.....T.....A.....C.....?.....G	
<i>S.oedipus</i>	T.....C.....C.....C.....A.....T.....C.....G.....C.....C.....C.....C.....C.....TA.....A.....C.....A.....T.....C.....?	
<i>S.tripartitus</i>	T.....C.....C.....C.....A.....T.....T.....C.....C.....C.....C.....C.....G.....T.....G.....C.....C.....T.....G	

[illegible]

400

[illegible]

HISTORICAL BIOGEOGRAPHY OF TAMARINS

# Appendix (continued)

	500
<i>C.goeldii</i>	GCCTTGTAGTATATAAGT-CAATACTCTGGTCTTGTAAACCAAAAATGGAG-AA--TACTTACTCCCTAGGGCAATC---AGGGAAAGAATAC--CTA
<i>C.jacchus</i>	.T.....T.....G.....C..C.G.....AT.C....A...G.....T--T..
<i>C.pygmaea</i>	.T...C.....T...T.....G.....C.G.....A.....C....TT--T..
<i>L.rosalia</i>	.T.....A..T.....G.....CAG..T.....CG.....T--C....G....C..--A..
<i>S.b.bicolor</i>	.....G-CC.....A.C.....G.G.C.....AAA-T--..T.....G....T
<i>S.b.martinsi</i>	.....G-CC.....A.C.....G..C.....AA--T--..T.....G....T
<i>S.b.ochraceus</i>	??T...T.....G....T
<i>S.f.fuscicollis</i>	.....C.....AC.....A.C.....G.G.?????????????????..C.....G..ATC.....C....
<i>S.f.fuscus</i>	????????????????????????????A.....G.....G--C.....C.....GC.ATC.....C....
<i>S.f.illigeri</i>	.....C.....AC.....A.C.....G.....GG--.....C.....G..ATC.....C....
<i>S.f.lagonotus</i>	.....C.....AC.....A.C.....G.....GG--.....C.....G..ATC.....C..TA..
<i>S.f.leucogenys</i>	.....C.....AC.....A.C.....G.....GG--.....C.....G..ATC.....C....
<i>S.f.melanoleucus</i>	.....C.....??G..ATC.....C....
<i>S.f.nigrifons</i>	.....C.....AC.....A.C.....G.G.....GG--.....C.....G..ATC.....C....
<i>S.f.weddelli</i>	.....C.....AC.....A.C.....G.G.....GG--T.C.....C.....GC.ATC.....C....
<i>S.geoffroyi</i>	.....AC-T.....A.C.....G.G.C..G..AAA-T--..T.....G....T
<i>S.imperator</i>	..T.....AC.....A.C.....G.....AA--T--..T.....G....T
<i>S.inustus</i>	??
<i>S.labiatus</i>	..?????..A.....A.C..GG.....G.G.....AA-T--..T.....G....T
<i>S.leucopus</i>	.....C.....A.....G.?..A.....AAA-T--..T.....A....CT
<i>S.m.midas</i>	.....GAC--..A.C.....G.G.....AG--T--..T.....G....T
<i>S.m.niger</i>	??T...T.....G....T
<i>S.m.mystax</i>	..T.....A.....A.C.....G.....AG--T--..T.....G....T
<i>S.m.pluto</i>	??AAC-T--..T.....G....T
<i>S.nigricollis</i>	.....C.....AC.....A.C.....G.....T.GG--.....C.....G..ATC.....C....
<i>S.oedipus</i>	.....C.....A.C.....G.G.C..G..AAA-T--..T.....G....C
<i>S.tripartitus</i>	????????????????????????????.....?..G.....GG--.....C.....G..ATC.....C..TA..
	↓ D-loop 600
<i>C.goeldii</i>	A-TTCTACCATCAACACCCAAAGCTGATATTCTAATA-TTAAACTACCCCTGAACAATAAAA-CAA-CA--TACT--ATTGGTGACTCAACAATAAAGT
<i>C.jacchus</i>	.....C.....T..T..T--CT--C.T--TTT..T....A..GACT.G.....G...
<i>C.pygmaea</i>	.....C.....T.....GC.....T.....C.T--CC--T..A--CC..T....A..A.GACT.G.....G...
<i>L.rosalia</i>	.....G.....G.....C..G.....TT..T.CT.....A..G.C.....C..G.G..
<i>S.b.bicolor</i>	.A.....A.....TT.....GGT.GCTT.TTTCGCTTCT..T....A..GTCC...CTC....
<i>S.b.martinsi</i>	.A.....A.....TT.....GGT..CTT..TT.GCTTCT..T....A..GTCC...CTC....
<i>S.b.ochraceus</i>	.A.....A.....AG.....??TT.....GGT..CTT..TT.GCTTCT..T....A?.GTCC...CTC....?
<i>S.f.fuscicollis</i>	.A.....A.....C.....TG.CT..C..GGT-CT..T....A..G..T.G..TC....
<i>S.f.fuscus</i>	.A.....A.....C.T.....TGGCC..C..GT-CT..T....A..G..G..TC....
<i>S.f.illigeri</i>	.A.....A.....G.C.T.....T.....TG.CT..C..GGT-CT..T....A..G..G..TC....
<i>S.f.lagonotus</i>	.A.....A.....C.T.....T.....TG.CT..C..GGT-CT..T....A..G..T.G..TC....
<i>S.f.leucogenys</i>	.A.....A.....C.T.....T.....TG.CT..C..GGT-CT..T....A..G..G..TC....
<i>S.f.melanoleucus</i>	.A.....A.???????..T.....TG.CT..C..GGT-CT..T....A..G..T.G..T....
<i>S.f.nigrifons</i>	.A.....A.....C.....T.....TG.CT..C..GGT-CT..T....A..G..T.G..TC....
<i>S.f.weddelli</i>	.A.....A.....C.....T.....GTG.CT..C..GGT-CT..T....A..G..T.G..T....
<i>S.geoffroyi</i>	.A.....G.....A.....G.....T.....A..CTTG.TTT.CTCT..T....A..GTCC...T....
<i>S.imperator</i>	.A.....A.....A.....TT.....G.T..CT..CT.GTCT..T....A..G.....T....
<i>S.inustus</i>	??
<i>S.labiatus</i>	.A.....A.....C.....TT.....CT..CT..GTCT..T....A..GT.....T....
<i>S.leucopus</i>	.A.....A.....TT.....TGG.TT..CTG.CTCT..T....A..GTCC...T.G....
<i>S.m.midas</i>	.A.....A.....A.....TT.....T..CTT.GTT..CTCT..T....A..GACG...TC....
<i>S.m.niger</i>	.A.....A.....A.....TT.....T..TT.CTT.GTT..CTCT..T....A..GACG...TC....?
<i>S.m.mystax</i>	.A.....A.....A.....TT.....CT..TT..GTCT..T....A..GT.....T....
<i>S.m.pluto</i>	.A.....A.....A.....TT.....CT..TT..GTCT..T....A..GT.....T....
<i>S.nigricollis</i>	.A.....A.....C.A.....T.....T..CC..C..GT-CT..T....A..G..G..TC....
<i>S.oedipus</i>	.A.....A.....G.....TT.....TTT.CTCT..T....A..GTCC...T....
<i>S.tripartitus</i>	.A.....A.....C.T.....T.....TG.CT????????????????????????????????



	700
<i>C.goeldii</i>	ACTTTACAAGTACGTATA--ACAC--CCAACTG-TCTATGTAA-TACGIGCAITTAATCTTAATCCCCATGAATAATGT-CAGTACTATAAA--TGCTTA
<i>C.jacchus</i>	....G.....T.C.....TT-T.....T.....TT.....GC.TTA.....A.AT.....T.....CA.....
<i>C.pygmaea</i>	....G.....C.C.....TTC.....T.....T.....TA.....G..TT.....ACATC.....T.....GA.....G
<i>L.rosalia</i>	....T.....T.....TTCT.TC.TGACCTC.....T.....?????????.....A.....C.A.....
<i>S.b.bicolor</i>	....G.....C.TA.G.....T.TT-T.....C-T.....A-T.....TA.....T.GC..GC.....A.....GG.....
<i>S.b.martinsi</i>	....G.....TA.G.....T.TT-T.....? -T.....A-T.....TA.....T.GC..G.....A.....GC.....
<i>S.b.ochraceus</i>	??
<i>S.f.fuscicollis</i>	.....CT.G--.TG.C-.T.-.T.AA-.....T.G..C.....A.....G
<i>S.f.fuscus</i>	.....CT.??
<i>S.f.illigeri</i>	.....ACT.G--.TG.C-.T.-.G-TC.....-G.....G..T.A.....C..A.....G
<i>S.f.lagonotus</i>	.....CT.G--.TG.C-.T.-.T.G-.....A.....G..T.A.....C..A.....C.....G
<i>S.f.leucogenys</i>	.....ACT.G--.TG.C-.A..-T..G-T.....GC.T.A.....C..A.....C.....G
<i>S.f.melanoleucus</i>	.....CT.G--.TGTC-.T.-.T.AA-.....T.G..T.....C..A.....A.....
<i>S.f.nigrifrons</i>	.....CT.G--.TGTC-.T.G-T.AA-.....A.....T.G..T.....C..A.....C.....
<i>S.f.weddelli</i>	.....T.CT--.TG.C-.T.-.T.AA-.....G.....T.G..T.....C..A.....C.....
<i>S.geoffroyi</i>	.....A..C--.T.TT-TTT-.T.-.G-T.....TA.....T.G..C.A.....A.G.....
<i>S.imperator</i>	.....G.....A.....T.TT-TA..-T..G-T.....TA.....G.C.T.A.....A.....GC.....
<i>S.inustus</i>	??
<i>S.labiatus</i>	....G.....A.....TA.T.TT-TA..-T..G-.....TA.....GC.C.A.....A.....CG
<i>S.leucopus</i>	....G.....A..C--G..TTAT.T-.T.-.G-T.....TA.....T.GC.CGC.....A.....
<i>S.m.midas</i>	?.?.?.T.....AC.C--..TT-TA..-T..G-T.....G-TA.....T.GCC.GC.....C.....
<i>S.m.niger</i>	??
<i>S.m.mystax</i>	.....A.....T-.T.TT-TA..-T..G-T.....TA.....G..T.A.....A.....GC.?????????
<i>S.m.pluto</i>	.....A..C.??
<i>S.nigricollis</i>	.....CT.G--.TG.C-.T.-.TA.G-T.....-T.....G..T.A.....G..A.....C.....G
<i>S.oedipus</i>	.....A..C--.T.TT-TTT-.T.-.G-T.....-TA.....T.GC.CGC.....A.G.....C.....
<i>S.tripartitus</i>	??
	800
<i>C.goeldii</i>	ATTATACAT??
<i>C.jacchus</i>	.C.....?GCACATAAAACCTTAA--CGTACATAAAACCTTGA?AAA?ATGC?TAT?AGC?AGA?CTGAAAA?ACCCCAATGGACCTTAACTTGCCAA
<i>C.pygmaea</i>	??
<i>L.rosalia</i>	.CC.....??
<i>S.b.bicolor</i>	.....GGCACATAGAACC-TAAACGTGCATATCAACTCCAGACAC-CATGCTTACAAACAAGTACTGT-AAAAGCTCATGAACCGCAAGACATTTCG
<i>S.b.martinsi</i>	.C.....AGCACAT-AAGTCC-AAACGTACATATGAATTCCGGCCAC-CATGCTTATAAGCAAGTACTAT-AAAAGTTTCATGAATTACAAGACATTITA
<i>S.b.ochraceus</i>	??
<i>S.f.fuscicollis</i>	..C.....AGTACATAAAACC-TAACCCTGCACATAAGATCCTTGCCAA-CATGCTTACAAGCAAGTACTAT-AAAACCATGGG-ACCAACACATCAA
<i>S.f.fuscus</i>	??
<i>S.f.illigeri</i>	..C.....??
<i>S.f.lagonotus</i>	..C.....AGTACATAAAACC-TAAACGTACATAAAA-TCCCCCCCRA-CATGCTTACAAGCAAGTACTAT-AAAGACACATGGA-ACCCACACATTCA
<i>S.f.leucogenys</i>	..C.....AGTACATGA?ACC-TAAACCACACATAAAATTCCTCCCCAA-CATGCTTATAAGCAAGTACTAT-AAAACCACATGGA-ACCAACACATCAA
<i>S.f.melanoleucus</i>	..C.....AGTAGATAAAACCC-AAACTGTACATAGAATCCCCCCCCAA-CATGCTTATAAGC?AGTACTGT-AAAACCACATGA?-GCCAACCCATTAA
<i>S.f.nigrifrons</i>	..C.....AGTACATAAAACC-TAAACCGTACATAA?ATCCCCCTCCAA-CATGCTTAC?AGC?AGTACTAT-AAAACCACATGG?-ATCAACACATTAA
<i>S.f.weddelli</i>	G.C.....AGTACATAAAACC-TAAACGTACATAAACAACCCCGAACAA-CATGCTTAT?AGC?AGT?CTGT-?AAACCACATGGG-ATCAACTCATCA
<i>S.geoffroyi</i>	.....GACACATTAAAGTCC-AAACGTACATAAACAACCTCCAGCCAA-CATGCTTACAAGCAAGTACTGT-AAAAGCTCATGAACATCAAGACATCAA
<i>S.imperator</i>	..C.....AGCACATAAAACCC-AAACGTACATAGCAACTCCCAACAA-CATGCTTACAAGCAAGTACTAT-AAAAGCTCATGAACCAAGACATCTCC
<i>S.inustus</i>	.C.....AACACATACAGCCC-AAACGTACATACAAACTCTTGCCAA-CATGCTTATAAGCAAGTACTGT-AAAAGCTCATGGACACAGGACATTITA
<i>S.labiatus</i>	.C.....AGCACATC-AACC-TAAACGTACATATTAAACCCAGCCAC-CATGCTTACAAGCAGGTACTGT-AAAAGCTCATGAACATCAAGACATTCC
<i>S.leucopus</i>	.....GACACATACAGTC-TAAACGTACATAAACAACCCCGAACAA-CATGCTTATAAACAAGTACTAT-AAAAGCTCATGGAATGCAGGACATCAA
<i>S.m.midas</i>	..C.....??
<i>S.m.niger</i>	??
<i>S.m.mystax</i>	??
<i>S.m.pluto</i>	??
<i>S.nigricollis</i>	.CC.....AGTACATAA?ACC-TAAACCGTACATAA?ATCCCCCTCCAA-CATGCTTATAAGC?AGTACTAC-AAAACCACATGG?-ATCTACACATTAA
<i>S.oedipus</i>	..C.....AGCACATTAAATCC-AAACGTACATAAATACTCCAGCCAA-CATGCTTATAAGCAAGTACTGT-AAAAGCTCATGGACTACAGGACATTAA
<i>S.tripartitus</i>	??

(continued)

# Appendix (continued)

		900
<i>C. goeldii</i>	..... ..... ..... ..... ..... ..... ..... ..... ..... .....	???
<i>C. jacchus</i>	??	???
<i>C. pygmaea</i>	??	???
<i>L. rosalia</i>	??	???
<i>S. b. bicolor</i>	ACTAGCTAGTTGACAGTAAAGGTACAGCACACGACTA-CCAAGCATGGC-----	???
<i>S. b. martinsi</i>	ACCAACTAATTGACAGTAAAGGTACAGCACACGACTA-CCAAGCATGGC-----	???
<i>S. b. ochraceus</i>	??	???
<i>S. f. fuscicollis</i>	ACCAAACTCCAATAGCCAAGATCCAC--CACATGAATATCCAACCAACTACTAAAAATTATGATCGTACATAGCGCATAAAATGAATGATCGAACATAG	???
<i>S. f. fuscus</i>	??	???
<i>S. f. illigeri</i>	??	???
<i>S. f. lagonotus</i>	ACCAAACTCGTATCAACAGAACTCAC--CACACGAATACCCAAACCAACCAATTAATACTCACTAAGCGTACATAGCACATGACATGAATAGTCGGACATAG	???
<i>S. f. leucogenys</i>	ACCAAAACCGTAACGAACAAGATTCCC--CACATGAATATCTAACAAACCATTAATA--TCATTAACTCGTACATGGTACATAAAAATGAATAATCGTACATAG	???
<i>S. f. melanoleucus</i>	ACTGAATCCCAACGACCAAGATTTC--CACACGAATATTAACCAACCACTAAAAATT?ATTAATCGTACATAGTACATAGAATGA?TAATCGAACATAG	???
<i>S. f. nigrifons</i>	ACTAACTCCAACAACCAAGATTAT--CACATGGATATCCAACCAACCAACCAAACTCATTGATCGTACATAGCACATAGAATGA?TGA?TGGACATAG	???
<i>S. f. weddelli</i>	ACCA?ATCTTAACAGCCAAGATCTAC--CACACGA?TATCCAACCAACCACTAAACTTCATTAACTCGTACATAGTACATGAGATGAATAATCGAGCATAG	???
<i>S. geoffroyi</i>	ACTGGCCAACCTTACAATAAAGGTACAGGACACGACTA-CCAAGCA-GAT-----	???
<i>S. imperator</i>	ACCAACAAATGACAGTAATAGGTACAGCACACGACTA-CCAAGCATGAT-----	???
<i>S. inustus</i>	?CTAAC?AATTGACATAATAGGTACAGCACACGACTA-CCAAGCATGG?-----	???
<i>S. labiatus</i>	GCCGGCCAGCGTACAGTAAAGGTACAGGACACACCTA-CCAAGCATGAT-----	???
<i>S. leucopus</i>	ATTAGCTATCTTACAATAAAGGTACAGGACACGACTA-CCAAGCAAGAT-----	???
<i>S. m. midas</i>	??	???
<i>S. m. niger</i>	??	???
<i>S. m. mystax</i>	??	???
<i>S. m. pluto</i>	??	???
<i>S. nigricollis</i>	ACCAAACTTCCAAAT?A?CAA?ATCCCCACATGA?TATCCAACAAGCCCAAAATTT?ATTAACCGTACATAGTACATAGAATGA?TGATCGGACATGG	???
<i>S. oedipus</i>	ATTAACCGATTACCAACAAAGGTACAGGACACGACTA-CCAAGCAAGAT-----	???
<i>S. tripartitus</i>	??	???
<i>C. goeldii</i>	..... ..... ..... ..... ..... ..... ..... ..... ..... .....	1000
<i>C. jacchus</i>	??	???
<i>C. pygmaea</i>	??	???
<i>L. rosalia</i>	??	???
<i>S. b. bicolor</i>	-----CATGACTATCCACAGGTATTATTGGTCTCTTAATCTACCAACCTCCG	???
<i>S. b. martinsi</i>	-----CATGACTATCCACAGGTATTATTGGTCTCTTAATCTACCAACCTC-G	???
<i>S. b. ochraceus</i>	??	???
<i>S. f. fuscicollis</i>	CACATCCTATTACGTAATCGTCCGGTCCATGGATATCCACAGGTATCATTGGTCTCTTAATCTACCAACCTCCG	???
<i>S. f. fuscus</i>	??	???
<i>S. f. illigeri</i>	??	???
<i>S. f. lagonotus</i>	CACATATCATTACGTAATCGTCCGGTCCATGGATATCC--CAGGTACCATTGGTCTCTTAATCTACCAACCTC-G	???
<i>S. f. leucogenys</i>	CACATTCATTACGT?ATCGT?CGGTCCATGGATATCCACAGGTATCATTGGTCTCTTAATCTACCAACCT???	???
<i>S. f. melanoleucus</i>	CACATCCTATTACGTAATCGT?CGGTCCATGGATATCCACAGGTATCATTGGTCTCTTAATCTACCAACCT???	???
<i>S. f. nigrifons</i>	CACATTCATTACGT?ATCGT?CGGTCCATGGATATCCACAGGTATCATTGGTCTCTTAATCTACCAACCTCCG	???
<i>S. f. weddelli</i>	CACATCCTATTACGTAATCGTCCGGTCCATGGATATCCACAGGTATCATTGGTCTCTTAATCTACCAACCTC-G	???
<i>S. geoffroyi</i>	-----TATGACTATCCAGCAAGTAACATTGGTCTCTTAATCTACCAACCTCCG	???
<i>S. imperator</i>	-----CATGACTATCCACAGGTGTAATTGGTCTCTTAATCTACCAACCTCCG	???
<i>S. inustus</i>	-----CATGACTATC?ACCAAGGTATTATTGGTCTCTTAATCTACCAACCTCCG	???
<i>S. labiatus</i>	-----CATGACTATCCACAGGTATTATTGGTCTCTTAATCTACCAACCTCCG	???
<i>S. leucopus</i>	-----TATGACTATCCACAGGTATTATTGGTCTCT?AATCTACCAACCTC-G	???
<i>S. m. midas</i>	??	???
<i>S. m. niger</i>	??	???
<i>S. m. mystax</i>	??	???
<i>S. m. pluto</i>	??	???
<i>S. nigricollis</i>	CACATCATATTACGT?ATC??	???
<i>S. oedipus</i>	-----TATGGATATCCAGCAGGTAACTGGTCTCTTAATCTACCAACCTCCG	???
<i>S. tripartitus</i>	??	???

Region of D-loop  
not sequenced.

1100

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C.goeldii      ??????????????????????ATTACTCTTGCATACCTCAAAATCAGCCCTTCAGAGAAGTGTACTTTATACTAATAC????????????????????
C.jacchus     ????????????????????????G.....C.?.....CA.T.....T.GCC..AG????????????????????
C.pygmaea     ????????????????????????G.....TC.....CG.TC..T.C-----GG-GGAGGGG??????????
L.rosalia    ????????????????????????G.....CA.A..C.....TTTA.....A.....T.C...CG.????????????????????
S.bicolor    A^AAATTAGTA-CTACCATGTCTGCC.....C..AT.....C.T.A.....C.A.....GCC..AA-A^AAA^A--CAACCAT
S.b.martinsi A^AAATTAGTA-CTACCATGTCTGCC.....C..AT.....C.T.A.....C.A.....T.GCC..AA-A^AAA^A--CAACCAC
S.b.ochraceus ????????????????????????G.....C.....GT.A.....AA.....GCC..AA-AGAAAA--CAACCAC
S.s.fuschicollis ACAAATCAGTAGT-ATCGTGTAGC..C....CC.....GT.A.....AA.....T.G.AA-AGAAGAGAGACACCCAC
S.f.fuscus   ????????????????????????G.....C.....GT.A.....AA.....T.AA-AGAAGAGAGACACCCAA
S.f.liligeri ????????????????????????G.....C.....GT.A.....AA.....T.T.G.AA-AGAAGAGAGATACCCAC
S.f.lagonotus ACAAACTAGTAAT-ACCATGTACG.C....CC.....GT..AT.....A??.....T.T.G.AA-AGAA?-GAGACCACCCAC
S.f.leucogenys ACAAAATTAGTAAT-ATCATGTACG.C....CC.....GT..AT.....AAG.....T.T.G.AA-AGAAGAGAACCGCCCAC
S.f.melanoleucus ACAAAATTAGTAGT-ATCATGTGCG.C....CC.....GT.A.....AA.....T.T.G.AAATAGAGAGGAGACACCCAC
S.f.nigrifons ?^AAATTAGTAAT-ATCGTGTACG.C....CC.....GT.A.....AA.....T.T.G.AA-AGAAGAGAGACTACCCAC
S.f.weddelli ??????T TAGTAGT-ATCATGTGCG.C....CC.....GT.A.....AA.....T.T.G.AATAGAGAGGAGACACCCAC
S.geoffroyi ACAAAATCAGTA-CGATCACACCTGTC.....C.....TG..C.T.....CAA.....C.T.G.AA-AGAGA----TCCCCP
S.imperator ACAAAATCAGTA-TTATCATATCTG.C....C.A.....T.C.....AT.....CAA.....T.AA-AGAAAG-CTCACCCAT
S.inustus   ????????????????????????G.....C.....T.C.....CAA.....T.AA-AGGAAA--CTTACTCAT
S.labiatius ACAAACTAGTAATTATTATATCCG.C....CC.....T.C.....CAA.....T.AA-AGGAAA--CTTACTCAT
S.leucopus  ????????????????????????G.....C.....T.C.....CAA.....T.AA-AGGAAA--CTTACTCAT
S.m.midias  A^AAATTAGTACTTGCCATGCTGTC.....CC.A.....C.T.....C.A.....GT.....AAGAAAAA--CAACCAC
S.m.niger   ????????????????????????G.....C.....T.C.....C.A.....GT.....AAGAAAAA--CAACCAC
S.m.mystax  ACAAACTAGTA-TTATCATATTCG.C....CC.....T.C.....CAA.....TC.T..AA-AGAAAA--TCTACTCAT
S.m.pluto   ????????????????????????G.....C.....T.C.....CAA.....TC.T..AA-AGAAAA--TCTACTCAT
S.nigricollis ACAAACTAGTAAT-ATCATGTGCG.C....C.....GT..A.....AA.....T.AA-AGAAGAGGAGACACCCAA
S.oedipus   ????????????????????????G.....C.T.....CAA.....C.T..AA-AGAGAA----TTCCGA
S.tripartitus ????????????????????????G.....C.T.....CAA.....T.T.AA-AA-AGAGAGACACCCAA
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1200

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C.goeldii      ??????????????ATCTAAGTACATTAAGTTAATGTAGCTTAATATCAAAGCAAGACACTGAAATGTCTAGACGGGT-ATCATTAACCCATAAA
C.jacchus     ??????????????????.CTC..A..ACCCG.....AT.T.....A...C.....
C.pygmaea     ??????????????????.TA.....GC.C.....CT.T.....G...C.....
L.rosalia     ??????????????????.T...A.TT.AC.....GT.T.....A..T..T..T..
S.b.bicolor   GTAAACTCA-TTACACCTTA.C..A...T.T.....?..?..T????????????????
S.b.martinsi  GTAAACTCA-TTACACCTTA.C..AC...A.....T.T.....????????????????
S.b.ochraceus GTAAACTCA-TTACACCTTA?C..AC...A.....T.T.....T...CA..GT.....??????
S.f.fuscolliis AAGAACCCCCC-GCAAC.C.C..A..C.G.....CT.T.....T...CAG.T.....??????
S.f.fuscus     AAGAACTTTCCCCACAAT.C.C..A.C..C.....T.T.....T...CAG.T.....??????
S.f.illigeri   AAGAACCTTCCTCACAAC.C...AC.A.C.G.....CT.T.....T...CAG.???..
S.f.lagonotus AAGGGTTTACCTCACAAT.C.C..A?..A.....CT.T.....????????????????
S.f.leucogenys AAGGACTTACCCACAAC.C.C..AC..A.....CT.T.....T...CA...C.....
S.f.melanoleucus AAGAACCTTCCTCACAAC.C.C..A.C..C.....CT.T.....T...CA..T.....??????
S.f.nigrifons  AAAAACCTTCCTCACAAC.CT...A.TT.AC.....GT.T.....T...CAG.T.....
S.f.weddelli   AAGAACCTTCCTCACAAC.C.C..A.C..C.....CT.T.....T...CA..T.....
S.geoffroyi    TACTGCCCACTATACTCC.A...ACC..A.....T.T...CG.....T...CAG..C.....
S.imperator    AACGCCCACTCCAC---C...AC..T..A.C.....T.T.....T...AG.T.C.....
S.inustus      AATAACCTA-CTCTAC--..C...A..T...C.....T.T.....T...AG.T.....??????
S.labiatus     AACGACCCACTATACTAC.C...T...C.....T.T.....T...CA..T.C.....
S.leucopus     ?????????????????????????????????????????????????????????????????????????????????????
S.m.midas      GGAGACTCACTACACCTC.G.C..A.....T.T.....T...A..A.....
S.m.niger       GGAGACTCACTTCACCTC.G.C..A.....T.T.....T...CA..A.....??????
S.m.mystax     AACGACCAATCAC--TAC.C...A..T...C.....T.T.....T...CAG.T.C.....
S.m.pluto      ??????????????TACTAC.C...T.....T.T.....T...CAG.T.C.....
S.nigricollis  AAGAACTTTCCCCACAAT.C.C..AC..A.....T.T.....T...CAG.T.....
S.oedipus      CACTGCCGACTATACTCC.A...ACC..A.....T.T.....T...AG..C.....
S.tripartitus  AAGGACTTACCCACAAC.C.C..A.C.....CT.T.....T...CAG.....

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